Fig. 3. Vertical section of the same, similarly enlarged.
Fig. 4. Vertical section of *Rosenella dentata*, Rosen, sp., enlarged twelve times. Silurian, Kattentack, Esthonia.
Fig. 5. Tangential section of the same, similarly enlarged.
Fig. 6. Vertical section of *Rosenella pachyphylla*, Nich., enlarged twelve times. Silurian, Kattentack, Esthonia.
Fig. 7. Tangential section of the same, similarly enlarged.
Fig. 8. Vertical section of *Rosenella macrocystis*, Nich., enlarged twelve times. Wenlock Limestone, Gotland.

PLATE II.

Fig. 1. Vertical section of *Labechia ohioensis*, Nich., enlarged twelve times. Ordovician (Hudson-River Formation), Cape Smythe, Lake Huron.
Fig. 2. Tangential section of the same, similarly enlarged.
Fig. 3. Tangential section of *Labechia serotina*, Nich., enlarged twelve times. Middle Devonian, Devonshire.
Fig. 4. Vertical section of the same, similarly enlarged.
Fig. 5. Vertical section of *Labechia canadensis*, Nich. & Mur., enlarged twelve times. Ordovician (Jewesche Zone), Saak, Esthonia.
Fig. 6. Part of an exfoliated specimen of *Labechia? Schmidtii*, Nich., enlarged about six times. Silurian (Upper Oesel Zone), Hoheneichen, Oesel.
Fig. 7. Tangential section of the same, enlarged twelve times.
Fig. 8. Vertical section of the same, similarly enlarged.

IV.—*The Origin of Metagenesis among the Hydromedusæ.* By W. K. BROOKS *.

MOST of the recent writers upon the origin of the sexual Medusæ which are set free from communities of sessile hydroids, and upon the relation between them and the hydroids, agree in the opinion that the sessile community is the primitive form, from which the Medusæ have been derived through division of labour, and the gradual specialization of the reproductive members of a polymorphic hydroid cormus.

In a monograph which has just been published in the 'Memoirs of the Boston Society of Natural History' ("The Life-history of the Hydro-Medusæ: a Discussion of the Origin of the Medusæ, and of the Significance of Metagenesis") I show that the life-history of the Narcomedusæ and Trachomedusæ is irreconcilable with this view. The accepted view regarding these groups of Medusæ is that they have been evolved from ancestors with a sessile hydra-stage and an alternation of generations, and that they have gradu-

* From the 'Johns Hopkins University Circulars,' No. 49, May 1886, pp. 86–88.

ally lost the hydra-stage, so that they now develop directly from the egg. I show that there is no reason for this opinion, but that we have in *Liriope* among the Trachomedusæ and in *Ægineta* and *Cunina octonaria* among the Narcomedusæ a true planula-stage and a true hydra-stage, although the hydra is simply a larva which develops into a medusa by direct growth and metamorphosis without alternation of generations. The life-history of these forms proves conclusively that the medusa-stage is older than the sessile hydroid cormus, which has arisen through the power to multiply asexually which is possessed by the hydroid larva of the medusa.

We have among the existing hydroids the series of stages in the origin of metagenesis which are represented in the following diagrams, in which the sign = denotes direct metamorphosis without multiplication, the sign × denotes asexual multiplication, and the sign $<$ denotes sexual multiplication.

In *Æginopsis,* as Metschnikoff shows, the egg gives rise to a ciliated swimming planula, which acquires a mouth and tentacles, and thus becomes directly and gradually converted into a floating hydra or *actinula,* which is at first ciliated like the planula. The tentacular zone of the floating hydra now grows out into a flange or umbrella, which carries the tentacles with it; sense-organs and a veil are soon acquired, and the hydra becomes a medusa.

The whole process is perfectly simple and direct; there is nothing like an alternation of generations, and the single egg becomes a single medusa with an actinula-stage, a floating, hydra-like, larval stage, and a swimming medusa-stage. The life-history is as simple and uninterrupted as that of any other animal which undergoes a metamorphosis, and it may be represented by the following simple diagram:—

I. ÆGINOPSIS: *Egg = Planula = Actinula = Medusa $<$ Eggs.*

As the floating hydra-stage of *Tubularia* is well known under the familiar name *Actinula,* and as it seems desirable to use a special term for the free hydra-stage of Medusæ as distinguished from a sessile hydroid, I shall employ this word for this purpose, designating by it a free or floating hydra, which may or may not be ciliated.

I have shown that we have in *Liriope* and its allies a life-history which is very similar to that of *Æginopsis,* with numerous secondary modifications, most of which are due to the fact that the gelatinous substance of the umbrella begins to be secreted between the endoderm and the ectoderm at a very early stage in the life of the embryo. The acceleration of the formation of the umbrella is exactly parallelled by innumerable similar phenomena in the lives of nearly all of the higher Metazoa, and it therefore presents no difficulties; and if we imagine the gelatinous substance absent, the mouthless, untentaculated, ciliated *Liriope*-larva is obviously a planula with an outer layer of ectoderm and a central capsule of endoderm. It has a spacious digestive cavity; the two layers are separated by a gelatinous substance; and in our species the cilia are restricted to a small part of the outer surface; but, in spite of these secondary modifications, it is clearly a planula. It soon acquires a mouth and four solid tentacles, and becomes converted into the floating hydra or actinula, with ectoderm, endoderm, stomach, mouth, lasso-cells, and four tentacles, but with neither subumbrella, sense-organs, nor veil. This larva becomes converted into an adult medusa by the growth of the tentacular zone into an umbrella, and by the acquisition of sense-organs, precisely like the *Æginopsis*-larva, and as each egg gives rise to only one adult, the life-history is simple and direct, with a planula-stage, a hydra-stage, and a final medusa-stage, and it may therefore be represented by the same diagram which was used for *Æginopsis*:—

II. Liriope: *Egg = Planula = Actinula = Medusa < Eggs.*

In our common American Narcomedusa, *Cunina octonaria*, the fact that the larva is a true hydra was long ago pointed out by McCrady. The planula-stage of this species has never been observed; but the resemblance between the ciliated, bitentaculated hydra and Metschnikoff's account of the *Æginopsis*-larva at the same stage is so close, that we have every reason for believing that in this species also the hydra-stage is preceded by a planula-stage without a mouth or tentacles. The hydra soon acquires two more tentacles, and is then fundamentally like the four-tentacled hydra of *Liriope*. The number of tentacles soon increases to eight, and the hydra becomes converted into a medusa by the outgrowth of the tentacular zone and the acquisition of sense-organs. So far the life-history of our *Cunina* is as simple as that of *Æginopsis* or *Liriope*; but it is complicated by the occurrence of asexual multiplication in the larva and also by parasitism. The actinula, or floating ciliated hydra, after gaining access to the subumbrella of a *Turritopsis*, gives rise to buds from the aboral end of its body, behind the circlet of tentacles; each of these buds is a hydra like the parent, and, like it, becomes directly converted into a medusa. As these secondary hydras originate as buds, they are at first sessile; but they become detached while in the hydra stage, or at least before they are completely converted into true medusæ. The time of detachment is not constant, and although the larvæ are at first sessile, and therefore not actinulas, they serve to show that the boundary-line between a floating actinula and a sessile hydra is an extremely faint one.

Owing to the occurrence of asexual multiplication, each *Cunina* egg may give rise to an indefinite number of adult medusæ; but as each larva becomes directly converted into a medusa by a process of growth, there is no alternation, and the life-history may be represented by the following diagram:—

Hydra=*Medusa*<*Eggs.*
×
III. Cunina octonaria: *Egg*=*Planula*=*Actinula*=*Medusa*<*Eggs.*
×
Hydra=*Medusa*<*Eggs.*

Here we have asexual multiplication without alternation; but in the *Cuninas* which Uljanin and Metschnikoff studied there is a true alternation which is obviously of secondary origin and undoubtedly due to a very slight modification of such a life-history as the one shown in diagram III. The planula itself is very peculiar and is furnished with an anomalous pseudopodial apparatus for clinging to and fastening upon the gastric process of the Geryonid within which it becomes a parasite; and the actinula or primary hydra into which it becomes converted never completes its development into a perfect free medusa. It remains as a brood-stock, from which other larvæ are budded, and these are set free and become converted into medusæ, so that the life-history is represented by the following diagram, in which for the first time we find a true alternation:—

IV. Cunina (Cunocantha) parasitica: *Egg*=*Planula*=*Actinula*× { *Hydra*=*Medusa*<*Eggs.* / *Hydra*=*Medusa*<*Eggs* / *Hydra*=*Medusa*<*Eggs.* }

A comparison of Metschnikoff's account of the development of *Cunina* (*Cunocantha*) *parasitica* and that which I have given of *Cunina octonaria* will bring out an interesting and significant difference between them which I have not yet pointed out. In the American *Cunina* the hydra-stage is well marked in the larvæ which are produced by budding as well as in the one which hatches from the egg. In Metschnikoff's species, however, the characteristics of the adult medusa begin to make their appearance in the secondary buds almost as soon as the buds themselves appear, and it would be difficult to recognize a hydra-stage in the life of this species if we were not acquainted with the simpler life-history of the American *Cunina*. In Metschnikoff's species the primary hydra is also greatly modified as an adaptation for its parasitic life, but in other respects its life-history is very similar to that of the ordinary hydroids; and if the acquisition of the medusa-characteristics by the secondary buds were a little more accelerated, so that their hydra-characteristics were entirely, instead of almost, crowded out, we should have a life-history like this:—

V. *Egg = Planula = Actinula* × { *Medusa* < *Eggs*. / *Medusa* < *Eggs*. / *Medusa* < *Eggs*. }

I know of no hydra which presents this life-history without modification; but there are many Campanularians and Tubularians in which the only modification is the acquisition by the actinula or primary hydra of the power to produce, in addition to the buds which become medusæ, other buds which remain in the hydra-condition, and share with their parent, the primary hydra, the power to produce both kinds of buds. Thus in *Perigonymus* (*Stomatoca*) the egg gives rise to a planula, which becomes the first hydra, and this produces other hydras like itself, and builds up a hydroid cormus; and ultimately all these hydras give rise to buds which become directly converted into medusæ, the hydra-like stage being completely suppressed; and we have a life-history like this:—

Hydra × { *Medusa* < *Eggs*. / *Medusa* < *Eggs*. }
×
Hydra × { *Medusa* < *Eggs*. / *Medusa* < *Eggs*. }
×
VI. *Egg = Planula = Actinula or Primary Hydra* × { *Medusa* < *Eggs*. / *Medusa* < *Eggs*. }
×
Hydra × { *Medusa* < *Eggs*. / *Medusa* < *Eggs*. }
×
Hydra × { *Medusa* < *Eggs*. / *Medusa* < *Eggs*. }

In *Turritopsis* we have essentially the same life-history, except that there is a secondary alternation between the primary hydra and the others. The planula does not become a hydra, but a mouthless untentaculated root, which is undoubtedly a degraded actinula or primary hydra. It does not give rise to medusa-buds, but remains as a brood-stock or embryonic hydra, from which fully-developed hydras are formed by budding; and all of these produce medusa-buds, so the life-history is as follows:—

$$\text{TURRITOPSIS: } \textit{Egg}=\textit{Planula}=\textit{Root}\times\left\{\begin{array}{l} \textit{Hydra} \times \left\{\begin{array}{l}\textit{Medusa}<\textit{Eggs.}\\ \textit{Medusa}<\textit{Eggs.}\end{array}\right. \\ \textit{Hydra} \times \left\{\begin{array}{l}\textit{Medusa}<\textit{Eggs.}\\ \textit{Medusa}<\textit{Eggs.}\end{array}\right. \\ \textit{Hydra} \times \left\{\begin{array}{l}\textit{Medusa}<\textit{Eggs.}\\ \textit{Medusa}<\textit{Eggs.}\end{array}\right. \end{array}\right.$$

In the ordinary Campanularians, with free medusæ, we have a new element of complexity, owing to the appearance of polymorphism. The ordinary hydras no longer give rise to medusa-buds, and these are produced only on the reproductive hydras or blastostyles. In *Eutima*, which I shall take as an example of this group, we have another complication which is very significant.

As in *Turritopsis*, there is a secondary alternation of generations, for, as I have shown above, the planula no longer becomes converted into a hydra, but forms a root from which the primary hydra is budded like those which appear later.

As I have shown, this secondary alternation occurs in many hydroids, such as *Hydractinia*, *Eutima*, *Turritopsis*, *Obelia* (Merejkowsky), and others, and it was correctly described by Wright in *Hydractinia* in 1856; but, so far as I am aware, no one has pointed out that it is a true alternation, exactly like the alternation between the hydra and the medusa, and that it is certainly a secondary acquisition, as we may see from the fact that in *Tubularia*, *Eudendrium*, and other hydroids the planula becomes directly converted into a hydra. So far as this point is concerned, the life-history of *Eutima* or *Hydractinia* and that of *Tubularia* or *Eudendrium* present the following contrast:—

$$\text{TUBULARIA: } \textit{Egg}=\textit{Planula}=\textit{Actinula}=\begin{array}{c}\textit{Hydra}\\ \times \\ \textit{Hydra}\\ \times \\ \textit{Hydra}\end{array}$$

with no alternation, while in the other forms we have

$$\text{EUTIMA: } \textit{Egg}=\textit{Planula}=\textit{Root}\times\left\{\begin{array}{l}\textit{Hydra}\\ \textit{Hydra}\\ \textit{Hydra}\end{array}\right.$$

with an alternation.

The complete life-history of *Eutima*, with its double alternation between the root and the hydranths, between the hydranths and the medusæ and its polymorphism, and division of the hydranths into nutritive persons and blastostyles, may be represented as follows:—

VII. Eutima: *Egg = Planula = Root* ×
- *Nutritive Hydra* ×
  - *Blastostyle* ×
    - *Medusa*<*Eggs.*
    - *Medusa*<*Eggs.*
    - *Medusa*<*Eggs.*
  - *Nutritive Hydra*
- *Nutritive Hydra* ×
  - *Nutritive Hydra*
  - *Blastostyle* ×
    - *Medusa*<*Eggs.*
    - *Medusa*<*Eggs.*
    - *Medusa*<*Eggs.*

In *Podocoryne* (*Dysmorphosa*) we have an extremely complex life-history, which, however, is readily derivable from one like that of *Eutima* as just given. There is a secondary alternation between the root and the hydranths, as in *Eutima*, and the polymorphism between the hydranths is more specialized, as we find not only nutritive polyps and blastostyles, but defensive polyps as well; and as each of the medusæ, in addition to its sexual function, also possesses the power to produce other medusæ by budding, the number of sexual animals which may be derived from a single egg is unlimited.

The following diagram represents the life-history of this species, except that the first generation of medusæ, like the second, gives rise to reproductive elements :—

VIII. Podocoryne: *Egg = Planula = Root* ×
- *Nutritive Hydra* ×
  - *Nutritive Hydra*
  - *Blastostyle* ×
    - *Medusa* ×
      - *Medusa*<*Eggs*
      - *Medusa*<*Eggs*
    - *Medusa* ×
      - *Medusa*<*Eggs*
      - *Medusa*<*Eggs*
  - *Defensive Hydra*

  ×
- *Nutritive Hydra* ×
  - *Nutritive Hydra*
  - *Blastostyle* ×
    - *Medusa* ×
      - *Medusa*<*Eggs*
      - *Medusa*<*Eggs*
    - *Medusa* ×
      - *Medusa*<*Eggs*
      - *Medusa*<*Eggs*
  - *Defensive Hydra*

  ×
- *Nutritive Hydra* ×
  - *Nutritive Hydra*
  - *Blastostyle* ×
    - *Medusa* ×
      - *Medusa*<*Eggs*
      - *Medusa*<*Eggs*
    - *Medusa* ×
      - *Medusa*<*Eggs*
      - *Medusa*<*Eggs.*
  - *Defensive Hydra*
- *Nutritive Hydra* ×
  - *Nutritive Hydra*
  - *Blastostyle* ×
    - *Medusa* ×
      - *Medusa*<*Eggs.*
      - *Medusa*<*Eggs.*
    - *Medusa* ×
      - *Medusa*<*Eggs.*
      - *Medusa*<*Eggs.*
  - *Defensive Hydra*

  ×
- *Nutritive Hydra* ×
  - *Nutritive Hydra*
  - *Blastostyle* ×
    - *Medusa* ×
      - *Medusa*<*Eggs.*
      - *Medusa*<*Eggs.*
    - *Medusa* ×
      - *Medusa*<*Eggs.*
      - *Medusa*<*Eggs.*
  - *Defensive Hydra*

  ×
- *Nutritive Hydra* ×
  - *Nutritive Hydra*
  - *Blastostyle* ×
    - *Medusa* ×
      - *Medusa*<*Eggs.*
      - *Medusa*<*Eggs.*
    - *Medusa* ×
      - *Medusa*<*Eggs.*
      - *Medusa*<*Eggs.*
  - *Defensive Hydra*

It is very probable that future research will show that even this complex diagram is too simple for some of the Hydromedusæ, and that there is, in some cases, a secondary alternation between the first generation of free medusæ and those which are produced by budding from this generation. The life-history of these proliferous medusæ has not been studied, as they are seldom found near laboratories and appliances for research; but there is reason to suspect that in some of them only the medusæ which are budded from the bodies of the medusæ of the first generation become sexually mature; and if future research should prove this, we should have still another alternation between the asexual proliferous medusæ and these sexual descendants.

In *Hydractinia*, the cormi of which are so similar to those of *Podocoryne* that a drawing of one will correctly represent the other, the life-history begins to simplify itself by the degradation of the sexual medusæ into sessile buds or reproductive organs, which, however, still retain traces of their former independent locomotor existence, traces which have almost totally disappeared in *Eudendrium* and in many of the Campanularians.

The life-history of *Hydractinia* may be represented as follows:—

	Nutritive Hydra ×	{ *Nutritive Hydra* *Blastostyle* × *Defensive Hydra* }	{ *Medusa Bud*<*Eggs*. *Medusa Bud*<*Eggs*. }
IX. HYDRACTINIA : *Egg* = *Planula* = *Root* × {	*Nutritive Hydra* ×	{ *Nutritive Hydra* *Blastostyle* × *Defensive Hydra* }	{ *Medusa Bud*<*Eggs*. *Medusa Bud*<*Eggs*. }
	Nutritive Hydra ×	{ *Nutritive Hydra* *Blastostyle* × *Defensive Hydra* }	{ *Medusa Bud*<*Eggs*. *Medusa Bud*<*Eggs*. }

Now what is the significance of this remarkable series of life-histories? Most of the facts have long been known; but the most conflicting interpretations of them have been advanced, and the student who seeks in the various monographs upon the subject an exposition of the relation between the direct development of a single adult from each egg, which is characteristic of most animals, and the circuitous history which is so remarkably exhibited by the medusæ, will find a speculative literature which is almost unlimited, but a total lack of agreement as to the true solution of this, the most interesting of all the problems involved in the life of these most interesting animals.

The view which I believe to be the true one is that the remote ancestor of the hydromedusæ was a solitary swimming hydra or actinula, with no medusa-stage, but probably with the power to multiply by budding. I believe that this pelagic animal gradually became more and more highly organized and more perfectly adapted for a swimming life, until it finally became converted into a medusa with swimming-bell and sense-organs, developing directly from the egg without alternation, but exhibiting during its growth the stages through which it had passed during its evolution. After this stage of development had been reached, I believe that the larva derived some advantage from attachment to other bodies, either as a parasite within other medusæ or as what may perhaps be called a semi-parasite upon other floating bodies, such as the fronds of algæ; and that it multiplied asexually in this sessile condition, giving rise to other larvæ like itself, all of which became medusæ.

I believe that the sessile or attached mode of life of the larvæ proved so advantageous to the species that it was perpetuated by natural selection, and that the primary larva then gradually lost its tendency to become a medusa, but remained a sessile larva, giving birth by budding to other larvæ which became sexual medusæ; that the medusa-characteristics of these secondary larvæ were accelerated, and that the primary larva gradually acquired at the same time the power to produce other larvæ, which remained permanently, like itself, in the hydra stage; that in this way the sessile hydra-communities with medusa-buds and free sexual medusæ were evolved; and that finally these communities became polymorphic, and that the sessile habit proved so advantageous that the free medusæ became degraded into medusa-buds or sexual buds on the bodies of the sessile hydras.

V.—*Endogenous as distinct from Exogenous Division in the Amœban Rhizopods.* By Surgeon-Major WALLICH, M.D.

I PROPOSE to show in this communication that whereas endogenous division in the naked Amœban Rhizopods is the prime factor in normal reproduction, exogenous division, in the majority of instances in which it is seen to take place during microscopic observation, is merely a mechanical disruption of the body-substance into two or more separate masses, produced accidentally by forces operating from